

# AGROCLIMATOLOGY

## Growth and Yield Response of Field-Grown Tropical Rice to Increasing Carbon Dioxide and Air Temperature

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### ABSTRACT

Although the response of rice (*Oryza sativa* L.) to increasing atmospheric CO<sub>2</sub> concentration and air temperature has been examined at the greenhouse or growth chamber level, no field studies have been conducted under the tropical, irrigated conditions where the bulk of the world's rice is grown. At the International Rice Research Institute, rice (cv. IR 72) was grown from germination until maturity for the 1994 wet and 1995 dry seasons at three different CO<sub>2</sub> concentrations (ambient, ambient + 200, and ambient + 300  $\mu\text{L L}^{-1}$  CO<sub>2</sub>) and two different air temperatures (ambient and ambient + 4°C) using open-top field chambers. Averaged for both seasons, increases in CO<sub>2</sub> concentration alone (+200, +300  $\mu\text{L L}^{-1}$ ) resulted in a significant increase in total plant biomass (+31%, +40%) and crop yield (+15%, +27%) compared with the ambient control. The increase in crop yield was associated with an increase in the number of panicles per square meter and a greater percentage of filled spikelets. Simultaneous increases in CO<sub>2</sub> and air temperature did not alter the biomass at maturity (relative to elevated CO<sub>2</sub> alone), but plant development was accelerated at the higher growth temperature regardless of CO<sub>2</sub> concentration. Grain yield, however, became insensitive to CO<sub>2</sub> concentration at the higher growth temperature. Increasing both CO<sub>2</sub> and air temperature also reduced grain quality (e.g., protein content). The combination of CO<sub>2</sub> and temperature effects suggests that, in warmer regions (i.e., >34°C) where rice is grown, quantitative and qualitative changes in rice supply are possible if both CO<sub>2</sub> and air temperature continue to increase.

AS THE GLOBAL DEMAND for energy and agricultural land increases, so will deforestation and the burning of fossil fuels. Since the mid-1800s, these human activities have contributed to an increase in atmospheric CO<sub>2</sub> concentrations from  $\approx 280 \mu\text{L L}^{-1}$  to a present-day concentration of  $360 \mu\text{L L}^{-1}$ , with projections of a  $600 \mu\text{L L}^{-1}$  CO<sub>2</sub> concentration by the end of the 21st century (Watson et al., 1990).

With respect to plant biology, there are two potential consequences of increasing atmospheric CO<sub>2</sub>. First, CO<sub>2</sub> can affect plant function, mainly through its direct effects on photosynthesis and stomatal physiology. Plants that possess C<sub>3</sub>-type photosynthesis and grow at less than optimal CO<sub>2</sub> levels can show dramatic increases in photosynthesis, growth, and yield as CO<sub>2</sub> rises (e.g., Kimball, 1983). Secondly, with a projected doubling of atmospheric CO<sub>2</sub> (in conjunction with increases in other greenhouse gases), several atmospheric general circulation

models (GCMs) predict an increase in mean surface temperature of several degrees (2.0–4.2°C; Schlesinger and Mitchell, 1985). Clearly, temperature affects a number of metabolic processes that influence growth and yield.

Most of the published studies on the impact of increasing CO<sub>2</sub> and air temperature have focused on temperate crops (Kimball, 1983). Far less attention has been given to important tropical plants (e.g., Hogan et al., 1991). Rice, for example, provides a substantial portion of calories for almost 1.6 billion people, with another 400 million depending on rice for a quarter to half of their diet (Swaminathan, 1984). Clearly, rice is a major food crop and the only major cereal used almost exclusively for human consumption. Because both CO<sub>2</sub> and air temperature can have marked effects on growth and yield, it is important to quantify the effects of these variables on tropical crops such as rice.

Several studies have examined the impacts of CO<sub>2</sub> concentration and air temperature on rice growth and yield in temperate regions under glasshouses or SPAR chambers (Imai et al., 1985; Baker et al., 1990, 1992; Ziska and Teramura, 1992a). However, no study has examined the interactions of increased CO<sub>2</sub> and air temperature for rice under irrigated field conditions in a tropical environment where most rice is grown.

In this study, we examined the growth and yield characteristics of rice grown at three CO<sub>2</sub> concentrations and two air temperatures during the wet (August–November) and dry (January–April) seasons using open-top field chambers in situ. Our objective was to quantify the growth and yield response of rice to increasing CO<sub>2</sub> concentration under tropical field conditions and to further determine if increasing air temperature modified the response to elevated CO<sub>2</sub>.

### MATERIALS AND METHODS

#### Controlled Environment Chambers

Experiments were conducted on a semidwarf rice (*Oryza sativa* L. cv. IR 72) using 18 open-top chambers (OTCs) established in an irrigated (paddy) field at the International Rice Research Institute (IRRI) in Los Baños, Philippines. Each chamber was assigned one of three different CO<sub>2</sub> concentrations (ambient; ambient + 200  $\mu\text{L L}^{-1}$ , intermediate CO<sub>2</sub>; and ambient + 300  $\mu\text{L L}^{-1}$ , high CO<sub>2</sub>) and one of two different air temperature levels (ambient and ambient + 4°C). Fixed levels of elevated CO<sub>2</sub> were not used, since ambient CO<sub>2</sub> can increase substantially during the night. All treatments (CO<sub>2</sub> and air temperature) were maintained over a 24-h time period

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throughout the experiment from germination until maturity. Sampling within an elevated chamber indicated that, at any given time during a 24-h period, the desired  $\text{CO}_2$  concentration did not vary by more than 10% from the set  $\text{CO}_2$  value and that the elevated air temperature was maintained within  $0.5^\circ\text{C}$  of the desired value. A typical daily response of  $\text{CO}_2$  concentration and air temperature is shown in Fig. 1. Average seasonal values (based on 24-h averages of  $\text{CO}_2$  concentration) corresponding to the three  $\text{CO}_2$  treatments (ambient, ambient + 200, ambient + 300  $\mu\text{L L}^{-1} \text{CO}_2$ ) were 369, 571, and 665  $\mu\text{L L}^{-1} \text{CO}_2$  (1994 wet season) and 364, 566, and 661  $\mu\text{L L}^{-1} \text{CO}_2$  (1995 dry season). Average mean air temperatures (based on 24-h averages) corresponding to the ambient and ambient +  $4^\circ\text{C}$  treatments were 25.6 and  $29.5^\circ\text{C}$  during the 1995 dry season. Mean air temperatures did not vary significantly between the wet or dry seasons.

Field chambers were octagonal, and constructed of Mylar polymeric film. Chambers were placed approximately 10 m apart; each chamber was 1.8 m high and  $3.5 \text{ m}^2$  in cross-sectional area, with a total air volume of  $\approx 6.0 \text{ m}^3$ . An extended frustrum with a  $0.35\text{-m}^2$  opening was attached to the top of each chamber to prevent wind intrusion and loss of  $\text{CO}_2$ . The chambers were designed to draw air down a vertical gradient through the canopy and then dissipate it through a large exhaust blower. A horizontal stream of  $\text{CO}_2$ -enriched air was injected above the canopy and mixed into the downward moving air stream. Inside the ductwork, air was circulated at 3.6 air changes per minute. If additional heating was required, air could be heated prior to injection by passing it over a set of

heating coils. A feedback control loop within the CR-10T datalogger (Campbell Scientific, Logan, UT) updated  $\text{CO}_2$  and air temperature values for each chamber. The  $\text{CO}_2$  concentration was measured every 6 min with infrared gas analyzers (Model LI-6252, Li-Cor, Lincoln, NE) set in an absolute configuration; air temperature was measured every 10 min with aspirated, shielded copper-constantan thermocouples set at canopy height within the chamber. Observations were recorded and evaluated by a CR-10T datalogger. If observations fell outside the desired limits, the datalogger sent a voltage signal through the SDM-AO4 (analog output) to proportional solenoid valves to adjust  $\text{CO}_2$  injection or to a solid-state controller to regulate temperature using simple feedback control algorithms. All  $\text{CO}_2$  and temperature data were downloaded to disk every 24 h (via an RS232 interface) for storage and retrieval. The data were used to generate operational control charts and to troubleshoot the system every 24 h.

Comparisons of microclimate within the ambient chamber and open field during the 1995 dry season indicated that the average air temperature difference was  $<1^\circ\text{C}$  (24-h values of 25.6 and  $25.2^\circ\text{C}$  for the ambient chamber and open field, respectively). On average, a chamber transmitted 85% of the incoming photosynthetically active radiation (PAR) relative to the open field at a plant height of 0.60 m for both growing seasons. Hourly values (0800–1700 h) of relative humidity obtained with a hand-held humidity sensor (Vaisala, Vantaa, Finland) over 5 d at plant height during booting (1995 season) showed no significant difference in relative humidity between ambient chamber and outside plots (data not shown).

Experiments were conducted during the 1994 wet season and 1995 dry season. Rice was sown on 26 July and 16 January for the wet and dry season, respectively. For each season, rice seeds (IR 72) were germinated in flats within each chamber at a given growth  $\text{CO}_2$ -temperature treatment. At 14 d after sowing (DAS), seedlings were taken out of the flats and placed in the ground within the chamber. Hills were placed at 20-by-20-cm intervals, three plants per hill (i.e., 75 plants  $\text{m}^{-2}$ , the usual plant density in commercial production in this environment). The area surrounding the chambers was also transplanted at this time at the same density. The overall statistical design was a  $2 \times 3$  factorial (two air temperature levels and three  $\text{CO}_2$  concentrations) with three replications in a randomized block design (RBD). Blocks were assigned randomly.

For each season, all standard cultural practices were followed. Nitrogen, as  $(\text{NH}_4)_2\text{SO}_4$ , was applied basally at a rate of 40  $\text{kg ha}^{-1}$  for the wet season and 60  $\text{kg ha}^{-1}$  for the dry season. After transplanting, timing of supplemental N was determined with a chlorophyll meter (SPAD Model 502, Minolta Corp., Japan) measurements. The actual amount of N added was determined using the relationship between uptake and cumulative degree days as given by Cassman et al. (1994). Total amounts of N added for the wet and dry seasons were 110 and 220  $\text{kg ha}^{-1}$ , respectively. Nitrogen was added either as  $\text{NH}_4\text{NO}_3$  or urea. All treatments for each season received the same amount of N at the same time.

### Growth and Yield Measurements

Destructive sampling of plant material began at 12 to 14 DAS, when plants were transplanted. Four to six hills per chamber were also sampled for both seasons at 36, 49, 68 DAS, at 50% flowering and at grain maturity. To determine the effect of the chamber itself on plant development, a similar number of hills was sampled in a separate plot (1 by 2 m) outside the chamber at each date during the 1995 dry season. No significant effect of increased  $\text{CO}_2$  (or the chamber itself) on the timing of flowering was observed. However, the ambient +  $4^\circ\text{C}$  treatment resulted in earlier flowering in both seasons

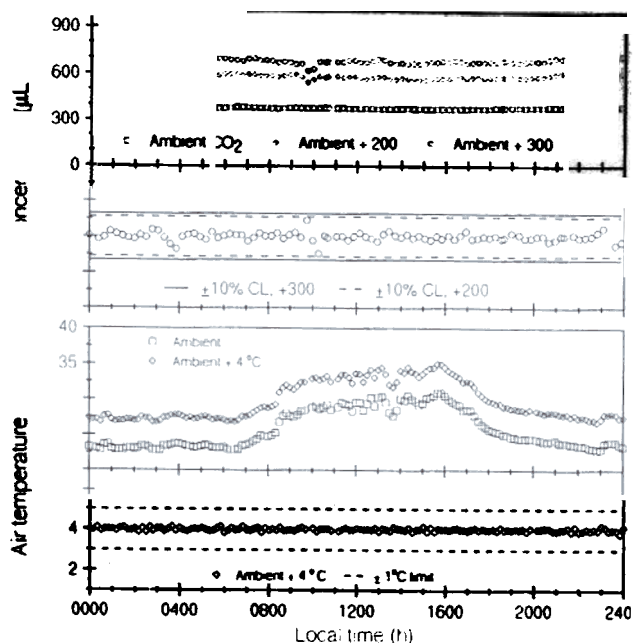


Fig. 1. Example of  $\text{CO}_2$  and temperature control over a 24-h period for individual open-top chambers during the 1995 dry season. Similar operating parameters were maintained for the 1994 wet season. Deviations from the set point are shown by the open circles ( $\text{CO}_2$ ,  $\mu\text{L L}^{-1}$ ) or diamonds (temperature,  $^\circ\text{C}$ ) at the bottom of each figure. CL (control limit) lines were  $\pm 10\%$  of the desired set point (e.g., if the desired set point for the ambient + 200 treatment was 560  $\mu\text{L L}^{-1}$ , an actual value of 530  $\mu\text{L L}^{-1} \text{CO}_2$  resulted in a deviation of  $-5.4\%$  for that treatment). Average seasonal values (based on 24-h averages of  $\text{CO}_2$  concentration) corresponding to the  $\text{CO}_2$  treatments (ambient, ambient + 200, ambient + 300  $\mu\text{L L}^{-1} \text{CO}_2$ ) were 369, 571 and 665  $\mu\text{L L}^{-1} \text{CO}_2$  (1994 wet season) and 364, 566 and 661  $\mu\text{L L}^{-1} \text{CO}_2$  (1995 dry season).

(77 vs. 81 DAS and 83 vs. 90 DAS for the high vs. the ambient temperature for the wet and dry season, respectively). At maturity (final harvest), 22 hills from each chamber and outside plots were sampled for final growth and yield analysis. Because of the earlier flowering times, maturity was earlier at the high air temperature (regardless of  $\text{CO}_2$  concentration) in both seasons. Except for sampling at maturity, plants were transplanted from outside the chambers to replace sampled hills after each sampling date. These plants did not come from the 1- by 2-m outside plot, and they were not sampled at later dates. This was done to prevent light gaps within the canopy.

At each sampling date, plant height was measured and the number of tillers was counted. Plants were then cut at ground level and separated into stems (culms) and leaf blades. Leaf area was determined photometrically with a leaf area meter (Li-Cor Model LI-3000). Leaves were kept between moist paper towels to prevent leaf rolling. Dry weights were obtained separately for leaf laminae, stems (including leaf sheaths), and panicles for both green and senesced material. Material was dried at  $70^\circ\text{C}$  for 72 h (or until dry weight was constant) and then weighed.

Because of the difficulty and destructiveness of root sampling, root biomass was determined only at transplanting, flowering and maturity. Prior to the start of each experiment, six cylindrical PVC tubes (20 cm in diameter, 30 cm deep) were filled with soil and placed within each chamber. These cylinders were perforated on the sides to prevent root binding. At flowering and again at maturity, plants were cut at soil level, pots were lifted from the soil, and any excess roots (i.e., those not within the volume of the pot) were removed. The soil was screened and washed, and roots were removed. The roots were then oven dried and weighed to estimate root dry mass per soil volume.

At maturity, in addition to the vegetative sampling described previously, grain yield, panicle weight, panicle/tiller ratio, percent filled grains, and 1000-grain weight were determined after

threshing and oven drying. Harvest index was then calculated as the ratio of grain yield (at  $140 \text{ g kg}^{-1}$  moisture) to total aboveground biomass. To determine potential changes in grain quality with increased  $\text{CO}_2$  and/or temperature, seed were then analyzed for percentages of  $\text{Ca}^{+2}$ , K, amylose, and protein.

For the 1994 wet season, between 13 and 14 October (during the grain-filling period), a typhoon caused minor damage to the open-top system and some lodging within the chambers. During this period, the  $\text{CO}_2$  and temperature control did not operate for 72 h while repairs were effected. All plants appeared to be affected equally.

All plant data were analyzed using a two-way ANOVA (LSTAT, IRR) comparing the effects of  $\text{CO}_2$  and temperature in combination. Duncan's multiple range test (DMRT) or Student's *t*-test was then used to separate treatment means. Unless otherwise stated, differences were determined as significant at the  $P \leq 0.05$  level.

## RESULTS

### Biomass Accumulation

Aboveground biomass was significantly increased by  $\text{CO}_2$  enrichment from ambient to ambient +  $300 \mu\text{L L}^{-1}$   $\text{CO}_2$  for both seasons, regardless of the growth temperature (Fig. 2). In both wet and dry seasons, significant differences between  $\text{CO}_2$  treatments were observed 14 to 20 d earlier for the high-temperature treatments (Fig. 2). Averaged over all  $\text{CO}_2$  treatments, an increase in growth temperature of  $4^\circ\text{C}$  resulted in earlier maturation of the crop by 5 and 6 d for the wet and dry seasons, respectively.

Overall, total biomass production at maturity was approximately 50% greater during the dry-season than during the wet-season experiment (Fig. 3). For both seasons, significant increases in total biomass (including

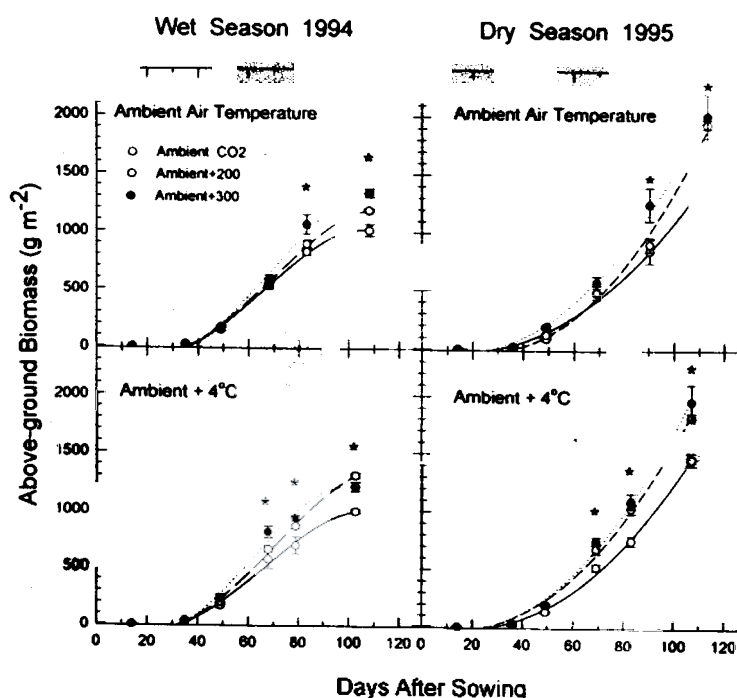


Fig. 2. Changes in aboveground biomass ( $\text{g m}^{-2}$ ) for the 1994 wet and 1995 dry season for rice (IR 72) grown at 3  $\text{CO}_2$  concentrations (ambient, ambient + 200, and ambient +  $300 \mu\text{L L}^{-1}$ ) and two temperature regimes (ambient and ambient +  $4^\circ\text{C}$ ). Bars indicate  $\pm 1$  SE. \* Significant difference between the highest  $\text{CO}_2$  concentration and the control for a given sampling date ( $P = 0.05$ , Student's *t*-test).

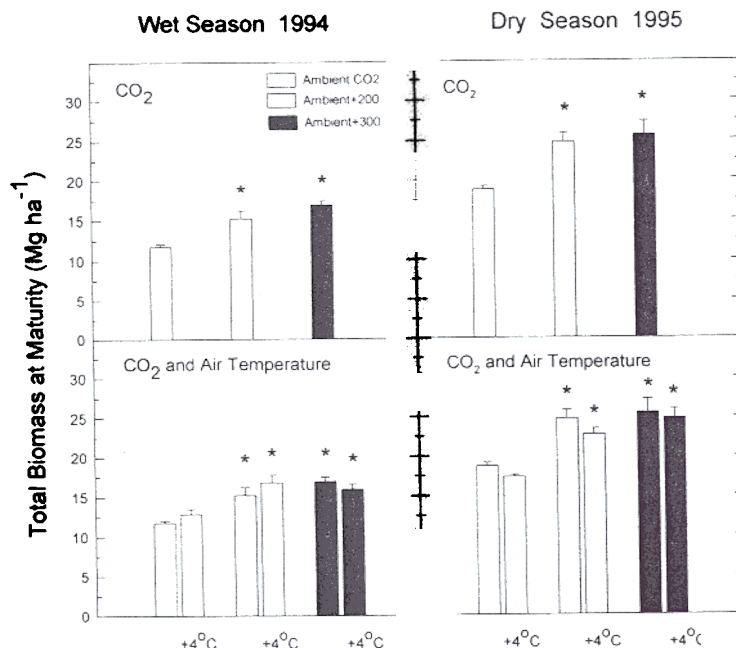


Fig. 3. Changes in total biomass (including roots) at maturity ( $\text{Mg ha}^{-1}$ ) for the 1994 wet and 1995 dry season for rice (IR 72) with increasing  $\text{CO}_2$  concentration (ambient, ambient + 200, and ambient + 300  $\mu\text{L L}^{-1}$ ), and increasing  $\text{CO}_2$  concentration at two different growth temperatures (ambient and ambient + 4°C). Bars indicate  $\pm 1$  SE. \* Significant difference between the highest  $\text{CO}_2$  concentration and the control ( $P = 0.05$ , Student's  $t$ -test). No interaction of increasing  $\text{CO}_2$  and temperature was observed.

roots) for both the +200 and the +300  $\mu\text{L L}^{-1}$   $\text{CO}_2$  treatments compared with ambient  $\text{CO}_2$  were observed (Fig. 3). No significant differences were observed between the two  $\text{CO}_2$  elevated treatments with respect to biomass production. Averaged over both seasons and both growth temperatures, the +200 and +300  $\mu\text{L L}^{-1}$   $\text{CO}_2$  treatments resulted in significant increases in total biomass relative to the ambient  $\text{CO}_2$  treatment (+31 and +40%, respectively). Although increased air temperature resulted in earlier maturation, no significant interaction of  $\text{CO}_2$  and temperature was observed for total

biomass production at maturity for the two growing seasons (Fig. 3).

### Growth Characteristics

Green leaf area (GLA) reached its maximum value at flowering for both seasons (Tables 1 and 2). Increases in leaf area with increased  $\text{CO}_2$  were observed early on (i.e., up to 49 DAS), but no consistent differences were observed at flowering or maturity. However, for each sampling date, the higher growth temperature (averaged

Table 1. Changes in growth parameters for the 1994 wet season for rice (cv. IR 72) grown at three  $\text{CO}_2$  concentrations and two temperature regimes.

Variable†	Time of sampling	Ambient temperature			Ambient temperature + 4°C		
		Ambient $\text{CO}_2$	+ 200‡	+ 300	Ambient $\text{CO}_2$	+ 200	+ 300
Leaf wt., $\text{g m}^{-2}$	MA		130	126		195	150
	FL		662b	1032a		1032a	863ab
	GLA		1596b	1809ab		1783ab	1952ab
			1365b	1356b		1837a	1552ab
			12.6b	11.5b		18.6a	15.1ab
Stem wt., $\text{g m}^{-2}$			75.2b	78.0b		110.6a	91.8ab
			246.0	286.6		257.4	279.7
			197.3b	194.9b		258.4a	226.2ab
			11.3ab	12.1a		16.6a	13.4a
			85.0c	104.6b		121.0a	102.1b
Root wt., $\text{g m}^{-2}$			504.8ab	613.9a		441.1b	491.5ab
			465.9b	573.0a		518.5ab	484.4ab
			333.0b	415.0a		345.0b	401.1a
			330.1a	353.8a		349.1a	381.3a
			0.28b	0.34a		0.31ab	0.29b
R/S			0.30ab	0.31a		0.28ab	0.34a

† GLA, green leaf area; FL, flowering; MA, maturity. All weights are dry weights. Stem weight is the dry weight of culm + leaf sheath. The root-to-shoot ratio (R/S) is the ratio of root to total aboveground biomass.

‡ + 200 and + 300: increase in  $\text{CO}_2$  concentration over the ambient level, in  $\mu\text{L L}^{-1}$ .

§ Within variables and rows, means followed by different letters are significantly different at the 0.05 probability level, according to Duncan's multiple range test.



**Table 2.** Changes in growth parameters for the 1995 dry season for rice (cv. IR 72) grown at three CO<sub>2</sub> concentrations and two temperature regimes.

Variable§	Time of sampling	Ambient temperature			Ambient temperature + 4°C		
		Ambient CO <sub>2</sub>	+ 200‡	+ 300	Ambient CO <sub>2</sub>	+ 200	+ 300
GLA, cm <sup>2</sup> hill <sup>-1</sup>			91c	144b	115bc		191a
			616c	828b	804b		924ab
			1540b	1740ab	2007a		2148a
			1046b	1103b	1349ab		1394ab
Leaf wt., g m <sup>-2</sup>			8.7c	13.6b	9.8bc		17.0a
			55.4bc	79.4a	66.2b		85.3a
			236.3b	304.0a	266.8b		312.1a
			287.3b	289.3b	301.4b		371.2a
Stem wt., g m <sup>-2</sup>			7.4b	12.8a	7.3b		15.9a
			71.5bc	116.3a	69.8b		114.3a
			564.1ab	650.0a	375.0c		629.4a
			589.2ab	635.3a	469.4b		683.6a
Root wt., g m <sup>-2</sup>			420.0b	519.5a	281.1c		321.0bc
			501.5a	516.5a	270.0c		489.1a
Root-to-shoot ratio			0.31a	0.29ab	0.27ab		0.31a
			0.23a	0.23a	0.16c		0.20b

† GLA, green leaf area; FL, flowering; MA, maturity. All weights are dry weights. Stem weight is the dry weight of culm + leaf sheath. The root-to-shoot ratio (R/S) is the ratio of root to total aboveground biomass.

‡ + 200 and + 300: increase in CO<sub>2</sub> concentration over the ambient level, in  $\mu\text{L L}^{-1}$ .

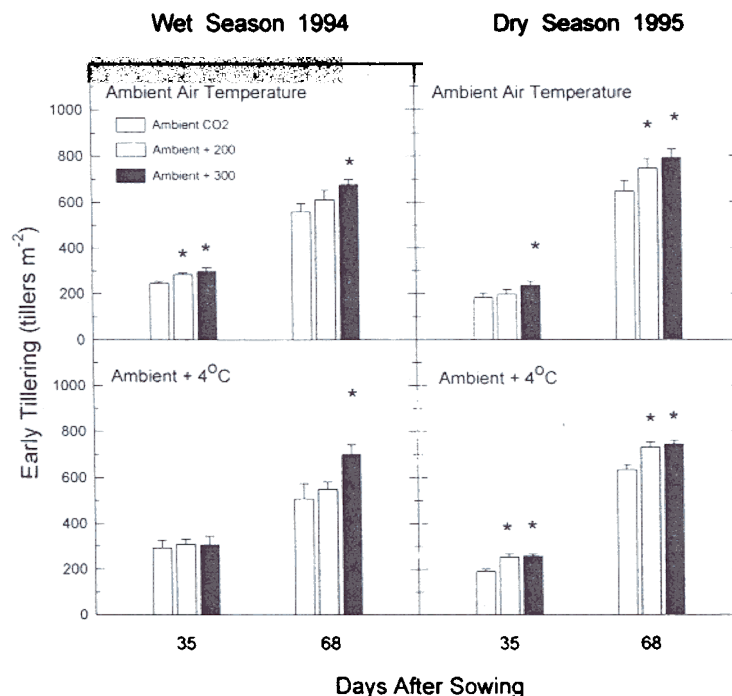
§ Within variables and rows, means followed by different letters are significantly different at the 0.05 probability level, according to Duncan's multiple range test.

over all CO<sub>2</sub> treatments) resulted in a significant increase in leaf area (Tables 1 and 2). A similar trend was observed for leaf biomass (i.e., both green and senesced leaves) with respect to CO<sub>2</sub> and temperature (Tables 1 and 2).

The overall response of tillering and biomass accumulation was similar. For the 1994 wet season, early production of tillers was increased with increasing CO<sub>2</sub>, with no significant effect of air temperature (Fig. 4). Not surprisingly, more tillers were produced during the 1995 dry season, but a similar response was observed with

respect to CO<sub>2</sub> concentration at ambient temperature (Fig. 4). Maximum tillering occurred in all CO<sub>2</sub> treatments and growth temperatures by 69 DAS. Small tillers were produced toward the end of both growing seasons, but these were ineffective in contributing to yield.

The sensitivity of stem biomass to increased CO<sub>2</sub> was consistent with the rise in tiller number. For the 1994 wet season, significant increases in stem biomass with increasing CO<sub>2</sub> concentration were observed for every sampling date (except at transplanting) until maturity at



**Fig. 4.** Change in tiller number for the 35 days after sowing (DAS) and 68 DAS sampling dates for rice exposed to increasing CO<sub>2</sub> concentration (ambient, ambient + 200, and ambient + 300  $\mu\text{L L}^{-1}$ ) at either ambient or ambient + 4°C growth temperature during the 1994 wet and 1995 dry season. Bars indicate  $\pm 1$  SE. \* Significant difference between the highest CO<sub>2</sub> concentration and the control for a given sampling date ( $P = 0.05$ , Student's *t*-test).

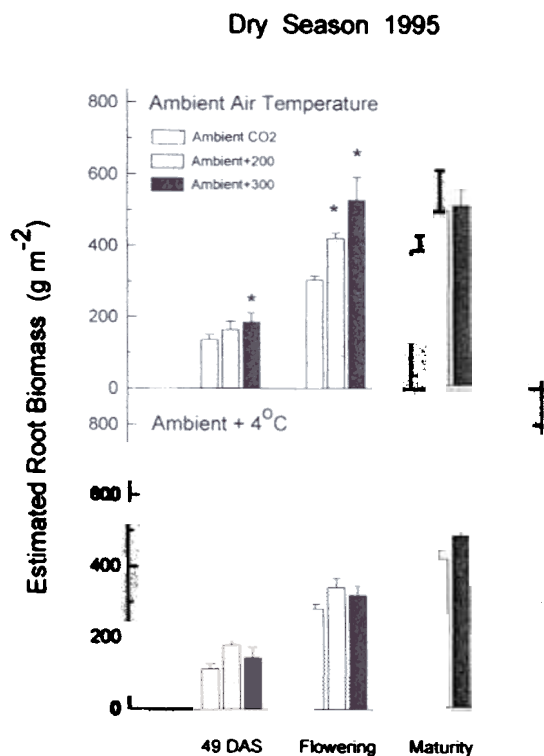


Fig. 5. Changes in estimated root biomass ( $\text{g m}^{-2}$ ) for the 1995 dry season for rice exposed to increasing  $\text{CO}_2$  concentration (ambient, ambient + 200, and ambient + 300  $\mu\text{L L}^{-1}$ ) at two different growth temperatures (ambient and ambient + 4°C) during the 1994 wet season. Bars indicate  $\pm 1$  SE. \* Significant difference between the highest  $\text{CO}_2$  concentration and the control ( $P = 0.05$ , Student's  $t$ -test).

the ambient growth temperature (Table 1). Similarly, at the elevated air temperature, increased  $\text{CO}_2$  resulted in increased stem weight until flowering. However, at elevated air temperature the stimulation tended to be significantly greater for the +200 than the +300  $\mu\text{L L}^{-1}$   $\text{CO}_2$  concentration (Table 1). For the 1995 dry season, significant increases in stem biomass with the highest  $\text{CO}_2$  concentration (i.e., ambient + 300  $\mu\text{L L}^{-1}$ ) were observed for both growth temperatures until maturity (Table 2).

Among growth parameters, root biomass showed the largest relative increase with increasing  $\text{CO}_2$  concentration. For the 1994 wet season, for example, root biomass at maturity increased 66 and 47% for the +300  $\mu\text{L L}^{-1}$  treatment relative to ambient  $\text{CO}_2$  for the ambient and elevated growth temperatures, respectively (Table 1). Similarly, for the 1995 dry season, a 32 and 81% increase in root biomass was observed with elevated  $\text{CO}_2$  for the ambient and elevated growth temperature (Table 2). Changes in root biomass were examined more thoroughly for the 1995 dry season. Beginning at 49 DAS, significant increases were noted in estimated root biomass at ambient temperature for the highest  $\text{CO}_2$  concentration (+300  $\mu\text{L L}^{-1}$ ) until maturity (Fig. 5). A similar result was obtained for the elevated growth temperature; however, at this temperature and at the intermediate (+200  $\mu\text{L L}^{-1}$

$\text{L}^{-1}$ )  $\text{CO}_2$  concentration, stimulated root growth was observed throughout the growing season.

The partitioning of biomass to the root relative to the shoot was significantly increased by increased  $\text{CO}_2$  concentration during flowering and maturity for the ambient and elevated growth temperature during the 1994 wet season (Table 1) and during maturity for both growth temperatures for the 1995 dry season (Table 2). No significant interaction was observed between increased growth temperature and  $\text{CO}_2$  concentration in their effect on biomass partitioning between root and shoot.

### Grain Yield, Components, and Quality

Grain yield responded to increased  $\text{CO}_2$  concentration to a lesser degree than did total plant biomass. Averaged over both seasons, the +200 and +300  $\mu\text{L L}^{-1}$   $\text{CO}_2$  treatments resulted in a significant increase in grain yield (15 and 27%, respectively) at ambient temperature (Fig. 6). For the 1994 wet season, a significant increase in grain yield was observed only for the +300  $\mu\text{L L}^{-1}$   $\text{CO}_2$  concentration, while both the intermediate and high  $\text{CO}_2$  concentrations increased grain yield significantly for the 1995 dry season (Fig. 6). If both  $\text{CO}_2$  and temperature are considered, however, the stimulation of grain yield with increased  $\text{CO}_2$  was entirely nullified at the elevated growth temperature (relative to the ambient  $\text{CO}_2$ -ambient temperature control) for both the wet and dry seasons (Fig. 6). Overall, as with biomass, dry season yields were substantially greater than those of the wet season.

Individual grain mass was fairly stable with respect to growing season or  $\text{CO}_2$  concentration; however, a significant decrease with temperature was observed (Table 3). Most of the increase in grain yield appeared to be associated with a significant increase in panicle biomass with increasing  $\text{CO}_2$  for both the wet and dry growing seasons (Table 3). This increase in panicle biomass was consistent with the change in percent filled spikelets as a function of  $\text{CO}_2$  for the 1994 wet season. As with panicle biomass, the percentage of filled spikelets declined significantly from the ambient to the elevated growth temperature. The overall reduction in percent filled spikelets for the 1994 wet season (compared with the 1995 dry season) was presumably due to effects of the typhoon. Interestingly, for the 1995 dry season, there did appear to be a synergistic effect between increasing  $\text{CO}_2$  and growth temperature with respect to a reduction in the percentage of filled spikelets. Because of the reduction in both panicle biomass and filled spikelets, harvest index (HI) was significantly reduced with increasing temperature for both seasons (Table 3). A slight, but nonsignificant, reduction in harvest index with increasing  $\text{CO}_2$  was noted (Table 3).

No change in percentages of  $\text{Ca}^{+2}$  or K were observed for the 1994 wet season as a function of either temperature or  $\text{CO}_2$  (Table 4); however, percent amylose, which determines the stickiness of rice, did increase with increasing growth temperature for the 1994 wet but not for the 1995 dry season. For both seasons, percent protein, which helps determine the nutritional quality of the rice grain, decreased with both increasing air temperature

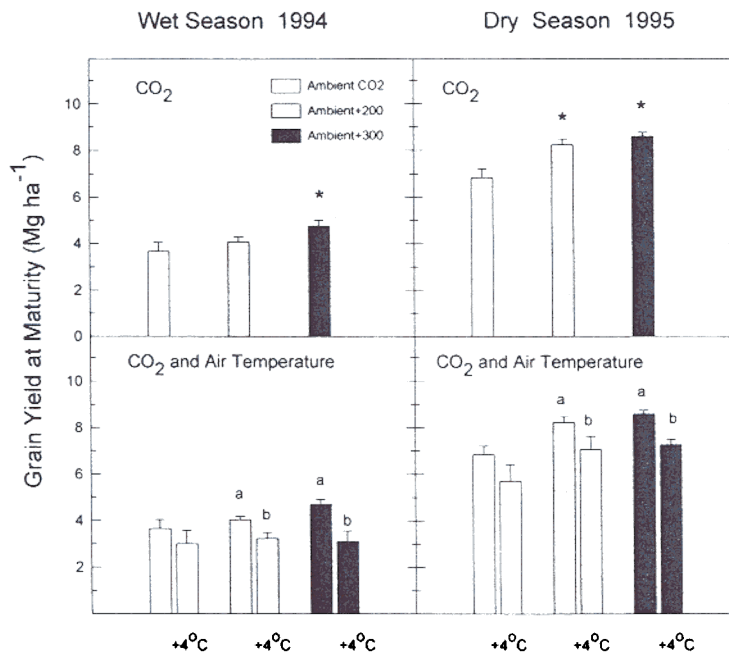


Fig. 6. Change in grain yield at maturity ( $\text{Mg ha}^{-1}$ ) for the 1994 wet and 1995 dry season for rice (IR 72) with increasing  $\text{CO}_2$  concentration (ambient, ambient + 200, and ambient + 300  $\mu\text{L L}^{-1}$ ), and increasing  $\text{CO}_2$  concentration at two different growth temperatures (ambient or ambient +  $4^\circ\text{C}$ ). Different letters indicate a significant reduction in grain yield relative to the ambient growth temperature at that  $\text{CO}_2$  concentration ( $P = 0.05$ , Student's  $t$ -test). Bars indicate  $\pm 1$  SE. \* Significant difference between the highest  $\text{CO}_2$  concentration and the control ( $P = 0.05$ , Student's  $t$ -test).

and increasing  $\text{CO}_2$  concentration. In analyzing grain quality, no interactive effects between  $\text{CO}_2$  and temperature were observed.

### Ambient Chamber vs. Outside Plots

Data obtained during the 1995 dry season indicate that total biomass and grain yield obtained at maturity were reduced 18 and 15%, respectively, for the ambient chamber treatment relative to the outside plots (data not shown). This reduction in productivity was presumably a result of the reduction in PAR for Mylar-covered experimental chambers (typically, PAR in the chambers was 85% of the outside ambient PAR), since little difference in growth temperature or relative humidity between the chamber and the outside plots was observed.

### DISCUSSION

The response of rice to increasing atmospheric  $\text{CO}_2$  has been examined under a wide range of conditions in phytotron, glasshouse, and SPAR unit studies (Imai and Murata, 1978; Imai et al., 1985; Baker et al., 1990, 1992; Ziska and Teramura, 1992a,b). The range of growth and yield responses to increased  $\text{CO}_2$  concentration have varied considerably, from 0 (Baker et al., 1992) to >50% (Imai et al., 1985; Baker et al., 1990). Changes in the abiotic environment, such as low solar irradiance or suboptimal air temperatures, have been suggested as a possible explanation (Baker et al., 1992); other possible sources of variation include cultivar (Ziska and Teramura, 1992a) and restricted root growth due to limited pot size (Arp, 1991). Because of such variation

Table 3. Changes in yield parameters at maturity for rice (cv. IR 72) grown at three  $\text{CO}_2$  concentrations and two temperature regimes, over the wet and dry growing seasons.

Variable†	Ambient temperature			Ambient temperature + $4^\circ\text{C}$		
	Ambient $\text{CO}_2$	+ 200‡	+ 300	Ambient $\text{CO}_2$	+ 200	+ 300
<b>1994 wet season</b>						
Panicle wt., $\text{g m}^{-2}$	449c§	529b	572a	371c	551ab	491b
1000-grain wt.	24.4a	24.7a	25.3c	22.8b	23.3ab	23.1b
% Filled spikelets	60.3c	64.0b	70.7a	49.3d	53.3cd	55.0c
HI	0.36a	0.35a	0.35a	0.31b	0.25c	0.26c
<b>1995 dry season</b>						
Panicle wt., $\text{g m}^{-2}$	726c	1076a	1099a	671c	854b	930ab
1000-grain wt.	24.8a	24.6a	24.9a	22.3b	23.4ab	23.4ab
% Filled spikelets	84.7a	84.8a	85.1a	82.4a	80.5ab	77.2b
HI	0.47a	0.42b	0.42b	0.39bc	0.39bc	0.36c

† HI, harvest index (grain weight divided by total aboveground biomass).

‡ + 200 and + 300: increase in  $\text{CO}_2$  concentration over the ambient level, in  $\mu\text{L L}^{-1}$ .

§ Within growing seasons and rows, means followed by different letters are significantly different at the 0.05 probability level, according to Duncan's multiple range test.

Table 4. Changes in grain quality parameters for rice (cv. IR 72) grown at two temperature regimes and three CO<sub>2</sub> concentrations, over the wet and dry growing seasons.†

Variable	Temperature (T)		CO <sub>2</sub>		
	Ambient T	Ambient T + 4°C	Ambient CO <sub>2</sub>	+200‡	+300
1994 wet season					
% Ca <sup>2+</sup>	0.09	0.08 <sub>ns</sub>	0.09	0.09	0.08 <sub>ns</sub>
% K	0.24	0.23 <sub>ns</sub>	0.24	0.22	0.23 <sub>ns</sub>
% Amylose	25.1	25.5*	25.3	25.3	25.4 <sub>ns</sub>
% Protein	10.2	9.4*	10.0	10.1	9.3*
1995 dry season					
% Amylose	26.4	26.3 <sub>ns</sub>	26.3	26.5	26.4 <sub>ns</sub>
% Protein	9.2	8.7*	9.3	9.2	8.4*

\* Significant at the 0.05 probability level, according to Student's unpaired *t*-test.

† Temperature data are averaged over all three CO<sub>2</sub> concentrations, and CO<sub>2</sub> data are averaged over both temperatures. No interactive effects were observed.

‡ +200 and +300: increase in CO<sub>2</sub> concentration over the ambient level, in  $\mu\text{L L}^{-1}$ .

in the response of rice, we thought it worthwhile to examine how, or even if, rice grown under irrigated field conditions in a tropical environment (i.e., typical conditions for more than 50% of the world's rice production) responds to elevated CO<sub>2</sub> over different growing seasons.

Although the absolute amount of biomass and grain yield increased substantially from the wet to the dry season, the relative enhancement of biomass and grain yield with increasing CO<sub>2</sub> at ambient temperature remained constant (e.g., a 30/31% and 44/40% stimulation of total biomass at maturity for the intermediate and high CO<sub>2</sub> treatments for the wet and dry seasons, respectively). Although the solar irradiance varies considerably between wet and dry seasons in the tropics (and explains in part, the absolute differences in productivity between seasons), low irradiance per se should not reduce the growth response to increased CO<sub>2</sub> concentration. This is because increased CO<sub>2</sub> can reduce or eliminate photorespiration, with a subsequent reduction in the light compensation point and apparent quantum efficiency for photosynthesis (Ziska and Teramura, 1992b). The relative stimulation of elevated CO<sub>2</sub>, therefore, is not necessarily reduced with low light (see Fig. 1 in Acocck et al., 1985). Similarly, while lower PAR within the chamber reduced rice productivity relative to ambient outdoor conditions, there is no reason to assume that the relative response of growth and yield to elevated CO<sub>2</sub> would be significantly different between chamber and field.

A saturating response of rice productivity to increased CO<sub>2</sub> was not always evident. For example, the relative stimulation of grain yield averaged for both seasons at ambient growth temperature was higher at the +300 than the +200  $\mu\text{L L}^{-1}$  CO<sub>2</sub> treatment relative to the ambient CO<sub>2</sub> control (+27% and +15%, respectively). This result differs from other studies, such as that of Baker et al. (1990), who found no response of grain yield to CO<sub>2</sub> concentrations above 500  $\mu\text{L L}^{-1}$ . Higher planting densities (e.g., 235 plants  $\text{m}^{-2}$  for Baker et al. 1990 vs. 75 plants  $\text{m}^{-2}$  for the current study) may have resulted in a reduction in average plant size (5 to 8 g plant<sup>-1</sup> for Baker et al., 1990 vs. 12 to 20 g plant for

the current study). It is conceivable that crowding could have affected the ability of rice yield to respond to additional CO<sub>2</sub> in an elevated-CO<sub>2</sub> environment.

Leaf area in rice, in contrast to other crops, does not appear particularly sensitive to CO<sub>2</sub> concentration. This is somewhat surprising, given the marked increase in tiller production as CO<sub>2</sub> increases (Baker et al., 1990; Ziska and Teramura, 1992a,b). However, other studies have shown that leaf number per tiller can be reduced with increasing CO<sub>2</sub> concentration with no net change in leaf area (Baker et al., 1990). Most of the aboveground increases in biomass, therefore, were associated with the response of tiller number to increased CO<sub>2</sub>.

The response of roots to increased CO<sub>2</sub> can also be quite striking (Rogers et al., 1992). From core sample data in this experiment, it was clear that root biomass responds readily to increases in CO<sub>2</sub> concentration. This was consistent with other studies suggesting that roots are a primary sink for additional C acquired under an elevated-CO<sub>2</sub> condition (Rogers et al., 1992). In general, partitioning of biomass to root systems increased with increasing CO<sub>2</sub> concentration at both flowering and maturity. Such increases have also been reported in other rice studies (Imai and Murata, 1976; Imai et al., 1985), as well as for wheat (Sionit et al., 1981).

Much of the increase in grain yield observed in this study was associated with increased tiller production and the subsequent increase in panicle weight. Increases in the number of grain-bearing spikelets are usually observed under CO<sub>2</sub> enrichment for rice as well as for wheat (Gifford, 1977; Sionit et al., 1981; Baker et al., 1990). In addition to increases in panicle weight, increases in the percent of filled spikelets with increasing CO<sub>2</sub> concentration were also observed during the wet season. Since increased CO<sub>2</sub> did not change the time period for grain filling (data not shown), the increase in percent filled spikelets was presumed to be due to greater assimilate transfer from leaves to spikelets during the grain-filling period for the high CO<sub>2</sub> treatments. Higher levels of leaf carbohydrate are commonly observed in elevated-CO<sub>2</sub> experiments (e.g., Yelle et al., 1989).

Given that increasing CO<sub>2</sub> results in significant increases in biomass and grain yield for rice, how was this stimulatory response altered by increasing growth temperature? At the biochemical level, photorespiration and subsequent C loss increase with temperature. Since elevated CO<sub>2</sub> reduces the amount of C lost via photorespiration, CO<sub>2</sub> and temperature should act in a synergistic fashion with respect to C assimilation and growth (for a discussion, see Long, 1991). In the current experiment, although higher growth temperatures resulted in faster biomass accumulation, earlier flowering times, and increased sensitivity to elevated CO<sub>2</sub>, no synergistic effect was observed between CO<sub>2</sub> and temperature with respect to biomass or grain yield. Other studies on the interaction of temperature and CO<sub>2</sub> concentration do not necessarily demonstrate a synergistic effect (Sionit et al., 1987a,b; Ziska and Bunce, 1994). It is possible that biochemical processes are not always expressed at the whole-plant or canopy level.

Grain yields were affected to a greater extent by tem-



perature than by CO<sub>2</sub> treatment. This is understandable, given that a sharp decline in fertile spikelets occurs at anthesis temperatures above  $\approx 31^{\circ}\text{C}$ . Data obtained in this study were consistent with a number of previous studies showing the sensitivity of flowering to high temperatures (e.g., Satake and Yoshida, 1978). Presumably, the reduction in the percentage of filled spikelets in the current experiment led to a decrease in panicle biomass and, ultimately, to a reduction in grain yield and harvest index with increasing growth temperature.

The degree of high air temperature-induced sterility (as determined from percent filled spikelets) was not reduced with increased CO<sub>2</sub>, but appeared to increase with increasing growth temperature and CO<sub>2</sub> level. Additional work is needed to elucidate this response, since pollen fertility was not measured directly. It is possible that, in this experiment, higher CO<sub>2</sub> levels resulted in reduced transpiration and a subsequent increase in canopy and panicle temperature for both temperature treatments.

In addition to grain yield, grain quality (% protein) also was affected by both temperature and CO<sub>2</sub> concentration. Reductions in grain quality as a result of increased CO<sub>2</sub> plus temperature need additional study, since changes in food quality as well as quantity have ramifications for rice production in tropical areas.

## CONCLUSIONS

Overall, the increase in atmospheric CO<sub>2</sub> concentration resulted in a significant increase in growth, total biomass at maturity, and grain yield for rice over two different growing seasons. The observed increase in biomass was due primarily to increases in tiller number and stem, root, and panicle weight. Data from this experiment indicate that, for both dry and wet seasons, a beneficial increase in growth and yield with elevated CO<sub>2</sub> per se is possible for irrigated rice grown in a tropical environment. If both CO<sub>2</sub> and air temperature increase simultaneously, however, any potential benefit of CO<sub>2</sub> on grain yield may be negated. In addition, increases in CO<sub>2</sub> and/or temperature may also reduce protein content and overall nutritional quality. Because future climates may have higher levels of both CO<sub>2</sub> concentration and temperature, additional work is needed to test for rice cultivars that could maximize reproductive productivity as atmospheric CO<sub>2</sub> increases, even if air temperature increases concurrently.

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